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DESCRIPTIONS OF NEW INTERGENERIC HYBRIDS BETWEEN CERTAIN CYPRINID FISHES OF NORTHWESTERN UNITED STATES.

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During the last eight years the senior author and numerous students in the school of fisheries, University of Washington, have collected fishes extensively throughout the Northwest. In many of these collections have appeared specimens which do not conform to published descriptions of any known species. They are either new species or hybrids.

To demonstrate with absolute certainty that these specimens are hybrids, would require experimental crossing of the two supposed parents. This we have not done, but our abundance of circumstantial evidence, statistically treated, indicates another clear case of hybridization in nature. Natural hybridization between different species and between different genera of fish probably is more common than usually believed. Hubbs and Schultz (1931 : 1-6), and Hubbs and Hubbs (1932 : 427-437), and others have observed natural hybridization.

Each hybrid is treated separately below.
I. Apocope oscula carringtoni Cope $\times$ Richardsonius balteatus hydrophlox (Cope).

The supposed hybrids, 19 in number, have been taken at the following localities in the State of Washington: Palouse River at Hooper, collected by L. P. Schultz and Leo Erkila, June 14, 1932; Palouse River at Palouse, collected by Schultz and Marvin Bowers on August 28, 1932; small tributary of the Palouse River 2 miles above Colfax, collected by Schultz and Erkila, June 18, 1932; South Fork Palouse River 2 miles above Pullman, collected by Schultz and Erkila June 15, 1932, and again on August 28, 1932, by Schultz and Bowers.

[^0]A study of the fish fauna of the Palouse River system above the falls, which are just below Hooper, indicates that the following species occur: A pocope oscula carringtoni; Richardsonius balteatus hydrophlox; Rhinichthys cataractae; Cyprinus carpio; Catostomus macrocheilus; Catostomus syncheilus; Pantosteus jordani; Esox vermiculatus; Aplites salmoides; Eupomotis gibbosus; Cottus rhotheus; and the supposed hybrid.

The reasons for suspecting that Apocope and Richardsonius are the parents of our supposed hybrids are: (1) In each locality where the hybrids were taken, large numbers of A pocope and Richardsonius were collected. (2) A survey of the Palouse River system fish fauna indicates that A pocope and Richardsonius are the only two species which could possibly be the parents of this supposed hybrid. Rhinichthys is very scarce and inhabits the upper parts of the colder and more turbulent waters and besides the hybrid does not resemble Rhinichthys. (3) Apocope and Richardsonius were taken from the same riffle in a spawning condition and in their breeding colors in late June of 1932, suggesting that these species spawn in the same part of the stream. (4) The supposed hybrid resembles both A pocope and Richardsonius in their general color and their general shape. (5) Our measurements and counts when treated statistically indicate that the supposed hybrid is either intermediate between the two supposed parent species or is not distinguishable from one or both of them in every detail studied.

Although numerous counts, measurements, ${ }^{2}$ and morphological characters were studied, the following did not give significant differences for the separation of Apocope oscula carringtoni from Richardsonius balteatus hydrophlox when treated statistically: Length from snout to origin of dorsal fin; length from snout to insertion of ventral fin; longest dorsal fin ray; longest anal fin ray; longest pectoral fin ray; longest ventral fin ray; length of caudal fin; length of the head; greatest depth of body; number of dorsal fin rays; number of pectoral fin rays; number of transverse rows of scales crossing the lateral line; number of scales above and below the lateral line.

Each character studied which was thought to indicate a valid difference between the parent species is treated in detail below.

1. The number of anal fin rays. Only the principal anal rays were counted, the two or three rudiments in front were omitted and the last two rays, usually branching from the single base were counted as one. Apocope oscula carringtoni had 7 anal rays in 119 specimens; there was no variation. Richardsonius balteatus hydrophlox had from 10 to 14 rays (mean $11.59 \pm .029$ ) in 249 specimens. The supposed hybrids had 8 or 9 anal rays in 19 specimens (mean $8.53 \pm 0.080$ ).
2. The number of pelvic fin rays. The last two pelvic fin rays, often branching from a single base, were counted as one ray. In 236 cases there were 7 to 9 (mean $7.93 \pm .012$ ) pelvic fin rays in Apocope oscula carringtoni and in 500 counts of Richardsonius balteatus hydrophlox, 8 to 10 (mean $8.78 \pm .013$ ) rays. The supposed hybrids had 8 to 10 (mean $8.83 \pm 0.050$ ) in 36 pelvic fin ray counts.

2 The counts and measurements were made by the junior author in most cases.
3. Pharyngeal teeth. The pharyngeal teeth were as follows: (The number not in parenthesis refers to the number of teeth and the number in parenthesis to the number of specimens possessing that number of pharyngeal teeth.) A pocope oscula carringtoni: Left side-4:0 (1); $4: 1$ (23); 4:2 (41). Right side-4:0 (2); 4:1 (22); 4:2 (39). Richardsonius balteatus hydrophlox: Left side-4:1 (10); $4: 2$ (29); $5: 1$ (18); $5: 2$ (51). Right side-4:1 (28); 4:2 (72); $5: 1$ (4); $5: 2$ (3). Hybrids: Left side-4:1 (1); $4: 2$ (4); $5: 2$ (2). Right side-4:1 (1); $4: 2$ (4); $5: 2$ (2). The above data indicate that in 108 specimen of Richardsonius balteatus hydrophlox, 64 per cent had five teeth in the main row on the left side while not a single Apocope oscula carringtoni had 5 teeth on either the left or right sides. Apocope occasionally had no teeth in the lesser row while in all examples of Richardsonius there were one or two teeth. The hybrids are intermediate, having either 4 or 5 teeth in the main row, and one or two in the inner row on both sides.
4. The general color pattern. Apocope oscula carringtoni: The body is variously covered on sides, belly and the back by numerous patches of brownish colored specks, each speck covers the exposed portions of one or two scales. The lateral band extends forward on the snout. It is pale over the region above the pectoral fin, but becomes rather dense posteriorly where it is as wide as the eye. Near the base of the caudal fin rays, the lateral band ends abruptly. A characteristic non-pigmented area occurs between the posterior margin of the lateral band and the caudal fin spot, which is very distinct on all specimens. Above and below the caudal fin spot, on the proximal third of the caudal fin rays are rows of blackish pigment which show up in a characteristic manner. The two pigmented areas, one on the upper lobe and one on the lower caudal lobe, are much less densely pigmented than the caudal fin spot. Along the base of the dorsal fin rays is a dark area which sharply contrasts with the light or whitish spot on the very base of the last one or two dorsal rays. In the hybrid this latter character is evident though fainter.

Richardsonius balteatus hydrophlox: A few widely scattered and rather small speckled areas may occur on the sides of the body but none occur on the back or on the belly as found on Apocope. The blackish lateral band is divided into a narrow upper and a wider lower portion by a slightly oblique light streak which is about as wide as the pupil. The upper dark band is widest over the pectoral fin and fades out posteriorly in the region below the posterior margin of the dorsal fin. The weakly pigmented lower band is about $2 / 3$ the diameter of the eye anteriorly, but posteriorly it becomes very blackish from the region over the pelvic fin to the base of the caudal fin rays where it ends abruptly. Along the axis of the body is a narrow thin blackish line, which cuts across the light lateral streak anteriorly and across the blackish lower band posteriorly. This line begins above the region of the pectoral fin. The pigmentation of the operculum appears to be a more or less continuation of the wide lateral band. Around the lower margin of the eye is a narrow sparsely pigmented area. The lateral band extends forward to the snout. The suborbital is unpigmented. On adults the belly is pinkish to orange, especially brilliant on the males
during the breeding season. The caudal fin spot is very faint, almost obsolete in the adults and young. Along the base of the anal fin rays is a series of black pigment spots, very faint in the hybrids.

Hybrids: The color in alcohol or formalin is brownish, with chocolate brown specks or freckles on sides and on the back, much as in Apocope, but fewer. The specks are more or less arranged in small patches and cover nearly the entire exposed portion of one or two scales. The specks are more closely packed dorsally; those on the sides are much scattered, as in A pocope, which it resembles very much in regard to this character. The blackish lateral band begins in the region over the pectoral fins, narrow at first but becoming as wide as $1 / 2$ the diameter of the eye below the dorsal fin and extending posteriorly to the base of the caudal fin rays where it ends in a wide expansion terminating at the posterior edge of the hypural plate. Anteriorly this lateral blackish band is cut across by a slightly oblique light streak, exactly as in Richardsonius but fainter. This light streak widens anteriorly, almost obliterating the lower lateral band. The dark narrow line, so obvious in Richardsonius, which extends along the axis of the body is in the same position on the hybrids but much fainter. The pink or orange belly of Richardsonius was not observed on the hybrids. This was to be expected since none of the hybrids appeared to be mature. A band of fine dots is present on the operculum and continues forward on the snout. The fleshy margin below the eye is somewhat pigmented too. The maxillaries and chin are pigmented as in both of the supposed parent species. The caudal spot is faint. It occurs just beyond the posterior edge of the fleshy caudal base of the caudal fin, near the base of the middle rays. This spot is intermediate in density between Apocope and Richardsonius. The proximal third of the caudal fin rays above and below the caudal fin spot are slightly pigmented, a character so obvious in Apocope. Along the base of the anal fin rays is a series of very faint pigment spots, which are very distinct in the young of Richardsonius. The color of the peritoneum is light dusky, nearly white ventrally, but becoming darker dorsally. It is finely speckled. In A pocope the peritoneum is dark brown to blackish while in Richardsonius it is silvery with brownish speckles not crowded.

In general, the color of the hybrid may be compared to two pictures having been recorded on the same film, with the picture of Richardsonius slightly dominating.
5. The presence or absence of a barbel. An examination of each specimen was made by means of a binocular microscope to determine the presence or absence of a barbel at the posterior tip of the maxillary. In Apocope oscula carringtoni a barbel was present in 141 specimens and absent on 20. In Richardsonius balteatus hydrophlox it was absent on all specimens. A barbel was present on the left side of only one of the supposed hybrids, and absent on all others.
6. Depth of the caudal peduncle. The least depth of the caudal peduncle was expressed in hundredths of the standard length as in the case of all other measurements. In 119 specimens of Apocope oscula carringtoni the range was from 10.0 to 14.9 (mean $12.33 \pm .048$ ) and in 252 specimens of Richardsonius balteatus hydrophlox from 8.0 to 10.4 (mean $9.37 \pm .018$ ).

15 specimens of the supposed hybrid have a range from 9.5 to 11.4 (mean $10.42 \pm .078)$.
7. Length of the caudal peduncle. The length of the caudal peduncle is the distance from the base of the last anal fin ray to the posterior tip of the hypural plate. In 119 specimens of A pocope oscula carringtoni the range was from 19.0 to 27.9 (mean $24.61 \pm .076$ ), and in 251 specimens of Richardsonius balteatus hydrophlox the range was from 17.0 to 23.9 (mean $20.26 \pm .051$ ). In 15 specimens of the supposed hybrid the range was from 20.9 to 27.6 (mean $23.70 \pm .310$ ).
8. Diameter of the eye. The eye was measured along the greatest diameter. In 113 specimens of Apocope oscula carringtoni the range was from 5.0 to 8.4 (mean $6.55 \pm .035$ ) and in 233 specimens of Richardsonius balteatus hydrophlox the range was from 6.5 to 10.4 (mean $8.64 \pm .043$ ). The range for 15 of the supposed hybrids was from 7.3 to 9.7 (mean 8.48 $\pm 0.164$ ).
9. Length of mouth. The length of the mouth was measured from the tip of the snout to the posterior edge of the maxillary. In 120 specimens of A pocope oscula carringtoni the range was from 5.0 to 7.9 (mean $6.70 \pm .027$ ) and in 252 specimens of Richardsonius balteatus hydrophlox from 7.5 to 11.4 (mean $9.48 \pm .028$ ). The range for the 15 supposed hybrids was from 7.25 to 9.7 (mean $8.68 \pm 0.135$ ).
10. Length of snout. The length of the snout is the distance from the tip of the snout to the anterior margin of the eye. In 120 specimens of A pocope oscula carringtoni the range was from 6.5 to 9.4 (mean $7.95 \pm .033$ ) and in 251 of the Richardsonius balteatus hydrophlox from 6.0 to 8.4 (mean $7.10 \pm .019$ ). The range for 15 of the supposed hybrids was from 6.4 to 9.1 (mean $7.58 \pm 0.134$ ).

The counts and measurements of these morphological characters of Apocope and Richardsonius overlap in certain cases. However, if all of these characters are considered together and the average differences between A pocope and Richardsonius are added together to form a character index, no overlapping occurs. This may be done in the following manner and expressed as an index similar to that used by Hubbs and Whitlock (1929:470) and Schultz and Welander (1934:5-6). Our character index is based on the following principle. If the mean of a given character in Apocope is significantly greater than the mean for the same character in Richardsonius the value is positive and is added to the other (positive) characters, but when the mean for a character in Apocope is significantly smaller than the mean in Richardsonius the value is considered negative and is subtracted from the other (positive) characters. This results in the addition of the numerous small average differences between the various characters for each specimen.

This concept was applied to our data and may be expressed more concisely for our case by the following formula:

Character Index $=$ Length of caudal peduncle + least depth of caudal peduncle + length of snout - diameter of eye - length of mouth the number of anal rays.

In the above character index we used only those characters which were found to give statistically significant differences between the supposed parent species when studied alone. This formula was applied to each individual specimen. The character index of 111 specimens of Apocope oscula carringtoni ranges from 19.0 to 32.9 (mean $25.64 \pm .168$ ) and of 249 specimens of Richardsonius balteatus hydrophlox from 2.0 to 13.9 (mean $7.26 \pm .105$ ). The 15 hybrids are almost intermediate between the parentspecies for they range from 12.9 to 18.9 (mean $15.90 \pm 0.300$ ).

The following method was used to determine the probability against the supposed hybrid falling within the variation of the supposed parent species for each character. The ratio of a given deviation from the mean of a frequency distribution to the probable error in a single observation represents the probability of the occurrence of a deviation as great or greater than the given deviation. Thus, for example (Table I) hybrid 15 , length of the mouth, it was found that the deviation from the mean of Apocope was 6 times the probable error of a single observation. This represents odds of 19,300 to 1 against the chance occurrence of this deviation within this frequency (length of mouth). The table of odds used by us was that presented by Hodgman (1933: 180). From that table ${ }^{3}$ we extract the following so that the reader may judge for himself the possible significance of our findings. Ratio of deviation to P. E. and odds against to one, 5.0 and 1,$341 ; 6.0$ and 19,$300 ; 7.0$ and $4.27 \times 10^{5} ; 8.0$ and $1.47 \times 10^{7}$; 9.0 and $7.30 \times 10^{8}$; respectively.

It may be seen from Table I that individual specimens of the hybrid may always be distinguished from both parent species by the number of anal rays and may usually be distinguished by the character index. An examination of Table II indicates further that the hybrid may be distinguished statistically from A. o. carringtoni on the basis of the depth of the caudal peduncle, the diameter of the eye, and the length of the mouth; that the hybrid may be distinguished from $R . b$. hydrophlox in the same manner on the depth of the caudal peduncle, the length of the caudal peduncle, the length of the mouth, and length of the snout.

We conclude, therefore, that the specimens which are intermediate between Apocope and Richardsonius are natural hybrids. We base our conclusions on the facts that these hybrids are intermediate in regard to: number of anal rays; number of ventral fin rays; number and arrangement of the pharyngeal teeth; general color pattern; the presence or absence of a barbel at the corner of the mouth; depth of caudal peduncle; and length of mouth. They are indistinguishable from Apocope in regard to length of the caudal peduncle and length of snout, and can not be separated from Richardsonius on the basis of the diameter of the eye.

[^1]TABLE 1. The ratios of the deviation of each hybrid, Apocope oscula carringtoni x Richardsonius balteatus hydrophlox,


* Indicates ratio of less than 5.0, that is odds of less than 1,341 to 1 . " Indicates no measurement was made.

Table il. The differences between the means of hybrids and PARENT SPECIES AND THE RATIO OF THESE DIFFERENCES TO THEIR PROBABLE ERROR.
(The number outside the parenthesis is the difference between means with the P. E. and the number in the parenthesis is the ratio of the difference to the P. E.)
A pocope oscula carringtoni: number of anal rays $1.53 \pm 0.080$ (19.1); least of depth of caudal peduncle $1.81 \pm 0.092$ (19.7); length of caudal peduncle $0.91 \pm 0.319$ (2.85); greatest diameter of eye $1.93 \pm 0.168$ (11.5); length of mouth $1.98 \pm 0.138(14.3)$; length of snout $0.37 \pm 0.138$ (2.68); character index $9.74 \pm 0.344$ (28.3).
Richardsonius balteatus hydrophlox: number of anal rays $3.06 \pm 0.085$ (36.0); least depth of caudal peduncle $1.05 \pm 0.080$ (13.1); length of caudal peduncle $3.44 \pm 0.314$ (11.0); greatest diameter of eye $0.16 \pm 0.170$ (0.94); length of mouth $0.80 \pm 0.138$ (5.80); length of snout $0.48 \pm 0.135$ (3.56); character index $8.64 \pm 0.318$ (27.2).

## II. Apocope oscula carringtoni Cope x Richardsonius balteatus balteatus (Richardson).

Hybrids of A pocope oscula carringtoni x Richardsonius balteatus balteatus were obtained as follows: four from a tributary of the Yakima River near Ellensburg May 27, 1926, collectors Hubbs and Schultz; one from Baker Creek, tributary to Powder R., Oregon, June 30, 1931, collectors Schultz and DeLacy; one from Umatilla R. at Rieth, Oregon, August 30-31, 1932, collectors Schultz and Bowers; and one from Latah Creek, 4 miles south of Spokane, Washington, Aug. 26, 1932, collectors Schultz and Bowers. The values of the measurements of these seven specimens are very similar to those given above for Apocope oscula carringtoni x Richardsonius balteatus hydrophlox but the number of anal rays average higher (one hybrid with 8 rays; 6 hybrids with 9 rays; one hybrid with 10 rays) which is to be expected since $R$. b. balteatus has an average of about 3 or 4 more anal rays than R. b. hydrophlox.
III. Acrocheilus alutaceus Agassiz and Pickering x Mylocheilus caurinus (Richardson).

Hubbs and Schultz pointed out in their paper (1931: 1-6) that two specimens, one collected by Dr. J. O. Snyder and the other by Schultz and DeLacy, were probably hybrids between Acrocheilus alutaceus and Mylocheilus caurinus. We now have a third specimen in the collection of fishes, School of Fisheries, University of Washington, which was taken by Daniel Merriman, September 2, 1933, in the Silvies River about 20 miles north of Burns, Oregon. This specimen agrees closely with the other two and further corroborates the conclusions of Hubbs and Schultz (1931).

## IV. Chconda cooperi Girard.

The figure of Cheonda cooperi Girard (Suckley 1860:362, pl. LXIII, $1-5$ ) has caused us much concern for a number of years as to just what it
really represents. Dr. G. S. Myers very kindly sent us the following description of Cheonda cooperi, taken from the holotype, No. 238, U.S.N.M. The measurements are given in millimeters and the figures in parenthesis represent the lengths expressed in hundredths of the standard length. Standard length 172 ; length of head 41 (24.0); diameter of eye 8.6 (5); length of snout 12.7 (7.4); tip of snout to rictus 11.4 (6.7); length of lower jaw to articulation 15 (8.7); greatest depth of body 42 (24.2); least depth of caudal peduncle 14 (8.2); number of anal rays $2-111 / 2$; dorsal rays $3-81 / 2$; ventral rays $1-9$ both sides; scales in the lateral line to end of hypural plate, left side 63 , right side 65 ; scales below the lateral line, 7 on both sides; and scales above the lateral line, left side 12, right side 13.

Our opinion that this fish may be a hybrid is based on the following reasons: although the lower Columbia River has had its fauna studied rather extensively yet no fish since Girard's time has ever been reported which closely resembles Cheonda cooperi. We think that it must occur rarely or it would have appeared in some of the collections made in that region. Among the 12 genera of Cyprinidae in the lower Columbia River, Cheonda cooperi resembles but four, namely Acrocheilus, Mylocheilus, Ptychocheilus, and Richardsonius. The other genera, Apocope, Siphateles, Rhinichthys, Oregonichthys, Tinca, Cyprinus, and Carrasius have less in common with Cheonda and for various reasons could not be considered as possible parents of this form.

Richardsonius balteatus balteatus probably is one of the parents because it has the largest number of anal rays (12 to 18) of any of the four genera (Acrocheilus, Mylocheilus, Ptychocheilus and Richardsonius), while C. cooperi has 11 (the last two rays, often branched at the base, are counted as one) and all the other four genera have 10 or fewer. Richardsonius has 16 dorsal rays. It is the only one of the four genera with fewer scales in the lateral line than $C$. cooperi, the former having 11 to $18-55$ to $65-$ 7 to 9 , and the latter with 12 to $13-63$ to $65-7$. Therefore we conclude that $R$.b. balteatus is one of the parents.

If C. cooperi is a hybrid, and Richardsonius b. balteatus is one of the parents, then the other parent should have (if fish hybrids represent more or less of a blending of the two parents and we believe they do, see Hubbs and Schultz l.c. and the first section of this paper) fewer than 11 anal rays probably 7 or 8 ; and about 8 dorsal rays; probably about $13-75-7$ scales. Not having seen the holotype we hesitate to speculate in regard to other characters.

Among the three possible genera (Acrocheilus, Mylocheilus and Ptychocheilus) the former species obviously is not the other parent because it has too many scales in the lateral line ( $20-81$ to $93-16$ ). There are (10) dorsal rays, and the mouth (see Suckley l.c. fig. 5) of Cheonda is not inferior in position and the lower jaw is not "chisel-like" as in Acrocheilus. Ptychocheilus has too many dorsal rays ( 9 or 10 ) and too many scales below the lateral line ( 16 to $20-68$ to $79-7$ to 9 ), besides the mouth or gape is too large, otherwise it resembles Cheonda fairly well. It has 8 anal rays and 9 or 10 dorsal rays. For Mylocheilus caurinus we find no serious objections which would exclude it from being the other parent. There are 8 anal and

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We conclude from the evidence given above that Cheonda cooperi probably is a hybrid, and that one parent is Richardsonius balteatus balteatus and that the other parent probably is Mylocheilus caurinus.

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[^0]:    ${ }^{1}$ The authors wish to thank Dr. C. L. Hubbs for the loan of some of the hybrids used n the preparation of this paper.

[^1]:    ${ }^{3}$ This table may be used to judge the significance of the differences, expressed in terms of their probable errors presented in Table II.

